17. Effects of Elevated CO_2 on Keystone Herbivores in Modern Arctic Ecosystems

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> Current atmospheric CO_2 enrichment represents a dietary change of the biosphere not precedented in the past 0.5 million years.
>
> —Körner 2000

17.1 Introduction

A central theme of this chapter is that elevated atmospheric CO_2 will directly alter growth and nutrient quality of arctic plants and will indirectly change climate, especially at high latitudes. Determining how this environmental change will affect arctic ecosystems requires an understanding of not only the physiological ecology of arctic biota but also the strength and nature of biotic interactions. For example, changes in plant abundance and quality associated with elevated atmospheric CO_2 could negatively affect herbivores and so alter the competitive interplay between species and, thus, the ecological community.

Since much has recently been written about the effect of elevated CO_2 on the physiology and ecology of arctic plant communities (Chapin et al. 1992; Oechel and Vourlitis 1996; Oechel et al. 1997; Dormann and Woodin 2002), in this chapter we primarily focus on the potential effects of these environmental changes on key consumers in arctic ecosystems, specifically herbivores. Thus, a second theme of this chapter is that elevated CO_2 will affect the interaction between herbivores in arctic ecosystems and their plant food supply. We primarily focus on keystone herbivores in extant arctic ecosystems because they provide important insights into the effect of changes in plant quality and quantity on herbivore populations, specifically, and on arctic ecosystems, in general.

17.2 Elevated Atmospheric CO_2 Will Change Climate Especially at High Latitudes

Carbon availability to plants has increased at least 30% during the past 150 years due to burning of fossil fuels and forest destruction; although the same level of increase in carbon availability has occurred historically, it took place over about 500,000 years (Petit et al. 1999). This acceleration of CO_2 enrichment with industrialization is projected to continue so that by the end of the twenty-first century the concentration of CO_2 in Earth's atmosphere will have doubled compared to preindustrial concentrations (IPCC 1996).

Increased availability of carbon affects plant growth (via fertilization) and plant quality, as discussed below. Besides this fertilization effect of CO_2 enrichment, increased atmospheric CO_2 will also contribute to global warming because CO_2 is one of the greenhouse gases (Crowley 2000). The effect of global warming on arctic ecosystems, the region north of the latitudinal treeline, is difficult to ascertain because many other components of the climate system besides the greenhouse gases will also change: for example, hydrological processes (Körner 2000). However, current predictions suggest that global warming will vary across the globe with relatively small changes in temperature near the equator and the most substantial changes (>4°C) occurring at high latitudes such as the Arctic. These types of large-scale increases in temperature in the Arctic would change the seasonal phenology of arctic biota (Penuelas and Filella 2001; Lucht et al. 2002), cause substantial changes in distribution and abundance of plants (Davis and Shaw 2001) and animals (Walker, Gould, and Chapin 2001), and perhaps alter the significant amount of carbon now stored in arctic soils, thus further elevating atmospheric CO_2 (Oechel and Billings 1992).

Changes in seasonal phenology would have profound effects on the fauna in arctic ecosystems. For example, the breeding season of many arctic herbivores coincides with periods of maximal availability of young plant tissue that is most nutritious (e.g., Raveling 1978; Sedinger and Raveling 1986; Prop and de Vries 1993; Gunn and Skogland 1997). Increased ambient temperature would increase plant growth rate and so not only reduce the time period during which high-quality immature forage is available (Ayres 1993) but also directly affect the nutrient quality of forage plants (Tolvanen and Henry 2001). This can create a phenological mismatch between consumer and consumed that negatively affects reproduction of consumers (Dunn and Winkler 1999; Both and Visser 2001) and, hence, their populations (Boyd and Madsen 1997; Prop et al. 1998; Inouye et al. 2000; Price and Root 2000; Lenart et al. 2002; Root and Schneider 2002).

The primary prediction regarding changes in plant distribution and abundance with climate change is that shrub-tundra and taiga communities will spread northward and replace tussock-tundra (Bliss and Matveyeva 1992). Such a change in plant communities would decrease the abundance of tundra graminoids that, in turn, would adversely affect populations of arctic grazers. For example, large-scale climatic variability associated with the North Atlantic Oscillation between 1928 and 1977 was significantly related to plant phenology and interannual changes in growth, fecundity, and population trends for seven species of northern ungulates (Post and Stenseth 1999). If habitat preferences of contemporary herbivores remain fixed as plant distribution and abundance change, then browsing mammals currently inhabiting taiga (e.g., moose, snowshoe hare) will likely replace browsing mammals currently inhabiting shrub-tundra (e.g., caribou) as well as vertebrate grazers (e.g., voles, lemmings, geese) in the Arctic (Bryant and Reichardt 1992; Kerr and Packer 1998; Walker, Gould, and Chapin 2001). Such a change in animal communities would seriously affect the economies of several human populations in the Arctic, especially those that depend on caribou (e.g., Inuit and Cree) and geese (e.g., Yupik Eskimo).

In the remainder of this chapter, we primarily focus on the direct effect of CO_2 enrichment on arctic ecosystems and not on the indirect effects of CO_2 enrichment, such as global warming (Chapin et al. 1992; Arft et al. 1999).

17.3 Effects of Elevated CO_2 on Growth and Nutrient Quality of Arctic Plants

Our understanding of how elevated CO_2 affects plant growth and quality is based largely on studies of plants that are endemic to mid-latitudes and not high-latitudes (Bazzaz 1990; Mooney et al. 1991). However, some studies (Table 17.1) have focused on the direct effects of elevated CO_2 on arctic plants in intact arctic ecosystems (reviewed by Oechel and Billings 1992; Dormann and Woodin 2002). Elevated CO_2 has a short-term (days to weeks) positive effect on plant productivity, but over longer timescales (months to years) there is often a complete homeostatic adjustment that results in similar rates of photosynthesis in plants exposed to ecologically relevant but different levels of ambient CO_2 (Tissue and Oechel 1987; Oechel and Vourlitis 1996). In general, these studies reveal that elevated CO_2 has relatively minor direct effects on photosynthesis and net primary productivity of arctic plants, with the level of plant response primarily depending on temperature, and water, and nutrient availability (Oechel and Billings 1992; Oechel and Vourlitis 1997).

Although elevated CO_2 has relatively minor direct effects on photosynthesis and net primary productivity of arctic plants, elevated CO_2 significantly changes plant quality (Bryant and Reichardt 1992). In general, the carbon/nitrogen ratio in plants increases with CO_2 enrichment (Ayres 1993; Cotrufo, Ineson, and Scott 1998; Körner 2000). Increased carbon availability is often used by plants to boost the amount of carbon-based secondary compounds, such as tannins, especially in C_4 woody plants (Jonasson et al. 1986; Bryant and Reichardt 1992), or fiber, as in C_3 plants (Ayres 1993). Nitrogen limitation is often associated with CO_2 enrichment so that plants have less tissue protein (Berendse and Jonasson 1992; Cotrufo, Ineson, and Scott 1998). Thus, from an herbivore's perspective, increased plant fiber or secondary compounds and decreased protein in plants grown in conditions of elevated CO_2 directly reduce the nutritional

Table 17.1. Effects of elevated atmospheric CO_2 on characteristics of arctic plants and the arctic ecosystem depend on timescale (short-term is days to months, intermediate is months to years, and long-term is decades to centuries). Symbols denote whether the plant or ecosystem response to elevated CO_2 was higher (+), lower (−), or the same (0) compared to a control (i.e., the plant or ecosystem exposed to ambient CO_2). Data are from Oberbauer et al. (1986), Tissue and Oechel (1987), Grulke et al. (1990), Mooney et al. (1991), and Oechel and Vourlitis (1996).

	Timescale of response		
Plant or Ecosystem Effect	Short-term	Intermediate	Long-term
Plant Effect			
Growth and Production			
Photosynthesis	+	0	0
Transpiration	+	0	0
Biomass production	+	+/0	?
Shoot growth	+	0	?
Root:shoot ratio	+	?	+
Tillering	+	+	?
Tissue composition			
Nitrogen concentration	−	−	−
Carbon:nitrogen ratio	+	+	+
Starch content	+	+	+
Ecosystem Effect			
Evapotranspiration	+	0	0
Net ecosystem flux	+	0	?
Net carbon storage	+	+/0	+/0
Soil enzyme activity	+	+/−	+/−
Soil solution nitrogen	−	−/0	−/0

quality of the plants (Ayres 1993). As discussed in the following sections, these changes in plant resource allocation associated with elevated CO_2 are predicted to affect growth and condition of herbivores, herbivore population dynamics, and reciprocal interactions between arctic herbivores and the plant communities upon which they depend.

Although we focus in this review on the direct effects of elevated CO_2 on plant quality and how this will affect certain herbivores, it is worth emphasizing that elevated CO_2 will directly and indirectly influence interactions between plants and herbivores. For example, the increased carbon availability to plants with elevated CO_2 will likely interact with the effect of elevated CO_2 on ambient temperature, precipitation, and nitrogen deposition and their effects on plant quality (Oechel and Billings 1992; Shaw et al. 2002). Increased ambient temperature would likely increase nutrient availability in the arctic ecosystem so that plants may then route available carbon to growth rather than the production of carbon-based fiber or secondary compounds. Increased ambient temperature would also directly affect herbivore energy and nutrient requirements, development, and survival. Thus, elevated CO_2 will certainly affect plant-herbivore interactions in several ways (Ayres 1993). We focus here on one dramatic effect of elevated CO_2 on plant-herbivore interactions: how changes in plant quality can directly affect keystone herbivores in arctic ecosystems.

17.4 Top-Down and Bottom-Up Processes: The Importance of Keystone Herbivores in Arctic Ecosystems

Understanding how elevated CO_2 will affect arctic ecosystems requires knowledge of how elevated CO_2 will directly influence plant growth and quality, and how these changes in plant growth and quality will, in turn, influence consumers in higher trophic levels. Biotic communities in arctic ecosystems are primarily organized in linear food chains with distinct trophic levels (i.e., "trophic ladders") rather than in food webs with less distinct trophic levels (i.e., "trophic webs") (Strong 1992). Since arctic ecosystems have relatively low species diversity (Hansell et al. 1998) and low annual primary production (Bliss 1986) and are organized in multiple trophic ladders, predicting how changes in primary producers will influence consumers should be relatively straightforward. However, even for the relatively simple arctic ecosystem, there are multiple controls on ecosystem processes that complicate our ability to predict the effect of such perturbations as elevated CO_2.

According to Drent and Prins (1987), the distribution and abundance of arctic herbivores is largely determined by "bottom up" processes, such as nutrient availability to plants. Thus, increased plant growth associated with elevated CO_2 would increase primary productivity, which in turn would support more herbivores. However, the simultaneous decrease in plant quality associated with elevated CO_2 would nutritionally challenge some arctic herbivores and likely compromise their ability to numerically respond to the predicted increase in plant growth (see Section 17.5).

There are also "top down" processes, such as herbivory and predation, in arctic ecosystems that are important in influencing how the biota responds to elevated CO_2. Arctic ecosystems are unusual in that some herbivores, such as geese, are "keystone" species (Kerbes, Kotanen, and Jefferies 1990; Jefferies 1999), which means that they have a significant and disproportionately large impact on the ecosystem (Paine 1966; Paine 1969; Power et al. 1996). Keystone species in other ecosystems are usually predators (e.g., sea otters, starfish) near the top of the food chain rather than mid-level consumers such as herbivores (Strong 1992; Bond 1994).

The role of geese as keystone species in arctic ecosystems is described in the next section. The important point here is that the population density of keystone herbivores in arctic ecosystems affects the relative strength of top-down and bottom-up forces. At high population densities, keystone herbivores exert strong top-down influences on forage plants that can lead to runaway consumption and destruction of the arctic vegetation (Jefferies 1997; Mulder and Ruess 1998; Jefferies 1999; Mulder and Ruess 2001; Handa, Harmsen, and Jefferies 2002). In contrast, at lower herbivore population densities, resources available to plants may limit their productivity, which then will exert strong bottom-up control of herbivore populations (Drent and Prins 1987). In short, keystone herbivores in arctic ecosystems are of central ecological importance and so must be considered when determining how elevated CO_2 affects arctic ecosystems.

17.5 Geese as Keystone Herbivores in Arctic Ecosystems and Trophic Cascades

Herbivores in extant arctic ecosystems include relatively small populations of large mammals (e.g., muskox, caribou), large and often cyclic populations of small mammals (e.g., voles, lemmings), resident galliformes (e.g., grouse, ptarmigan), and migratory waterfowl (e.g., geese and a few duck species) (Bliss 1975; Batzli et al. 1980; Bliss 1986; Jefferies et al. 1992). Muskox and caribou are the only two ungulate species that are resident in the northernmost regions of the world (Klein 1986). Muskox are relatively unselective, bulk feeders that can eat plants high in fiber, whereas caribou are selective grazers whose performance is strongly affected by forage quality (White 1983; White and Fancy 1986; Lenart et al. 2002). Voles and lemmings are also selective grazers, their population dynamics are directly influenced by plant quality and quantity, and their grazing can have dramatic affects on the habitat (Batzli et al. 1980; Batzli 1983; Oksanen 1983; Bliss 1986). Grouse and ptarmigan, as well as medium-sized mammals such as arctic hares, do not occur at sufficiently high enough densities in arctic ecosystems to have major impacts on the vegetation (Batzli et al. 1980).

For the purposes of this review, we have chosen to focus on geese that inhabit primarily coastal salt marsh and adjacent uplands in arctic ecosystems for three main reasons: (1) avian herbivores such as geese require relatively high-quality forage and so changes in plant quality, like those predicted to occur with elevated CO_2, should rapidly affect their distribution and abundance; (2) coastal regions, in general, and those in the arctic, in particular, are especially vulnerable to changes in sea level like those predicted to occur with elevated CO_2 and global warming; and (3) geese are keystone species in this system (Kerbes, Kotanen, and Jefferies 1990; Jefferies 1999) that can consume as much as 90% of the net aboveground primary production (Cargill and Jefferies 1984). Thus, we focus on arctic-nesting geese because these keystone herbivores and their primary habitat are both likely to respond sensitively to the environmental change predicted with elevated atmospheric CO_2.

Body size is thought to put limits on the quality of foods that can be eaten by herbivores. In general, as body size of herbivores declines so does the fiber level of the selected diet and the proportion of energy requirements satisfied by energy yield from fermentation (Illius and Gordan 1993; Cork 1994). This pattern of decline in reliance on fiber with decreasing body size in vertebrate herbivores is thought to occur because of unequal allometries of energy requirements and gut capacity (Demment and Van Soest 1985). The relative rarity of avian herbivores (i.e., only 3% of extant bird species) suggests these allometric constraints are especially difficult to circumvent for birds (McWilliams 1999). True geese are exceptional birds in that they eat leaves throughout their life cycle and they are strong flyers with associated high metabolic rates. Thus, adult geese and especially their goslings are expected to respond sensitively to changes in plant quality and quantity because they require a relatively high quality and quantity of forage to satisfy their relatively high energy and nutrient requirements (McWilliams 1999).

Evidence for geese as "keystone herbivores" in arctic ecosystems (Kerbes, Kotanen, and Jefferies 1990; Jefferies 1999) includes the effect of their grazing on plant primary production (Cargill and Jefferies 1984; Bazely and Jefferies 1985; Jefferies 1988a; Hik and Jefferies 1990; Gauthier et al. 1995; Person, Babcok, and Ruess 1998) and on plant succession (Bazely and Jefferies 1986; Drent and van der Wal 1999); further evidence includes the dramatic effect of changing density of geese on the plant community (Mulder, Ruess, and Sedinger 1996; Srivastava and Jefferies 1996; Zacheis, Hupp, and Ruess 2001; Person et al. 2003) and the ecosystem properties (Ruess, Hik, and Jefferies 1989; Bazely and Jefferies 1997; Jefferies 1999).

Overgrazing by lesser snow geese has caused large-scale, long-term changes in quality and quantity of preferred arctic plants in coastal salt marshes throughout southern Hudson Bay and James Bay, Canada (Kerbes, Kotanen, and Jefferies 1990; Jefferies 1997; Handa, Harmsen, Jefferies 2002). This large-scale impact of geese on the vegetation is primarily the result of improved survival and habitat on the wintering areas (in the mid-southern U.S.), which has effectively removed what historically was the primary, density-dependent limitation on arctic-nesting goose populations (Batt 1997). These large-scale effects of overabundant geese on arctic plant communities has, in turn, negatively affected goslings attempting to grow up in arctic breeding areas with reduced plant quality and quantity (Cooch et al. 1991; Cooch, Rockwell, and Brault 2001).

The positive feedback responses between grazing goslings and their forage plants that occur at low to moderate grazing intensities break down at higher grazing intensities (Jefferies 1999). Destructive removal of below-ground parts of plants and overgrazing of above-ground plant parts by geese creates bare patches of sediment (Fig. 17.1), which then become hypersaline during summer due to increased rates of soil evaporation (Srivastava and Jefferies 1996). The hypersaline soil conditions depress growth and inhibit recolonization of the saltmarsh graminoids so that an alternative vegetational state develops that is dominated by *Salicornia borealis*, a salt-tolerant plant species that is not eaten by geese and persists for many decades. This process is called a "trophic cascade" by ecologists and refers to runaway consumption and dominance by species at higher trophic levels (in this case by geese) that has dramatic effects through the food chain (Jefferies 1999). Trophic cascades are rare in terrestrial systems, but when they do occur they are found where species diversity is low and food chains are linear: for example, in arctic ecosystems (Strong 1992).

Clearly, understanding how elevated CO_2 will affect arctic ecosystems requires

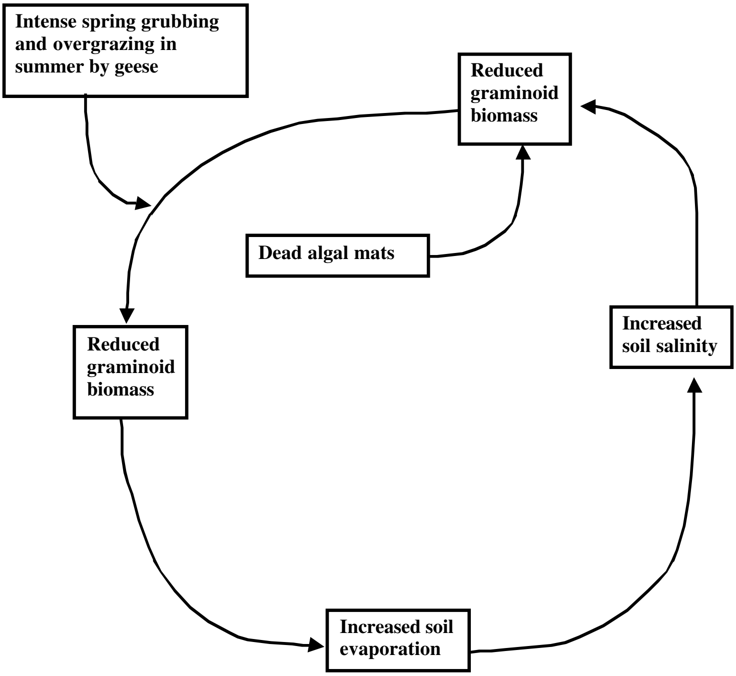


Figure 17.1. Overgrazing and grubbing by arctic-nesting geese in the low arctic salt-marsh ecosystem of Hudson Bay, Canada, has led to reductions in plant cover, increased soil evaporation, and salinity and thus to further reduction and degradation of the salt-marsh ecosystem. This trophic cascade has led to dramatic, large-scale changes in coastal salt-marsh vegetation from a vegetation community that supported large populations of vertebrate herbivores to a system with few if any plants palatable to herbivores. Geese are clearly keystone herbivores in this system and so must be considered when determining the effects of elevated CO_2 on arctic ecosystems. Modified from Srivastava and Jefferies (1996) and Jefferies (1999).

knowledge of how changes in plant growth and quality affect the keystone herbivores that dominate this ecosystem. We expect keystone herbivores such as geese to respond sensitively to changes in plant growth and quality because of the allometric constraints associated with being a bird that flies and eats leaves.

17.6 Reciprocal Interactions Between Plants and Herbivores in Arctic Ecosystems

In this section and the next, we discuss the interplay between arctic herbivores and their food plants and emphasize how changes in food quality affect plant-herbivore interactions. The reciprocal interactions between arctic herbivores and their food plants demonstrate how changes in plant quality, like those predicted to occur with elevated CO_2, can affect key consumers in arctic ecosystems.

In arctic ecosystems, plant chemistry (e.g., secondary compounds) controls herbivory on woody vegetation (Bryant and Kuropat 1980; Batzli 1983), and deciduous woody plants that are browsed respond to herbivory by changing their plant chemistry (Bryant and Reichardt 1992). Vertebrate herbivores such as the arctic hare browse deciduous woody plants (i.e., they eat shoots and leaves) whereas insect herbivores eat primarily just the leaves. When deciduous woody plants are browsed, more nutrients (e.g., nitrogen) are available for the remaining shoots so that leaf growth increases and available carbon is used to support increased plant growth rather than the production of carbon-based secondary compounds. In contrast, when leaves are repeatedly eaten from deciduous woody plants by insect herbivores, fewer nutrients are available for new leaf growth. This limitation of nutrients causes a surplus of available carbon that can be used to support increased production of secondary compounds or fiber. Thus, woody plants that are browsed are higher in quality (i.e., more nitrogen, less secondary compounds) than are woody plants that are defoliated by insects, and these differences in quality subsequently influence future herbivory (e.g., Danell and Huss-Danell 1985).

The interplay between arctic plants and herbivores is also evident for vertebrate grazers that eat herbaceous (nonwoody) plants. For example, flocks of arctic-nesting brent geese revisit certain areas of coastal salt marsh at intervals of time that maximize plant quality and quantity—a phenomena known as "cyclic grazing" (Prop 1991; Rowcliffe et al. 1995; Drent and van der Wal 1999)). Given the time required for plants to recover from being grazed and the intake rates achieved by brent geese on swards of certain biomass, the frequency of revisitation by these geese coincided with that which maximized their intake on a given sward (Fig. 17.2). Thus, cyclic grazing by brent geese effectively increased the amount of high-quality forage plants available to the geese within a season (Drent and van der Wal 1999).

Moderate grazing by geese increases the quality of forage because newer, younger plant tissue is higher in nitrogen and lower in fiber than is older tissue (Fig. 17.3). For example, grazing by lesser snow goose goslings increased net aboveground primary productivity by up to 100% and increased nitrogen concentration in forage plants, in large part because the droppings produced by feeding goslings increased available nitrogen for plant growth (Cargill and Jefferies 1984; Bazely and Jefferies 1985). Thus, goslings modulate nitrogen flow in this arctic ecosystem by their grazing and so increase the quality and quantity of available forage (Jefferies 1988a; Jefferies 1988b; Jefferies 1999).

17.7 Reduced Plant Quality like that Predicted to Occur with Elevated CO_2: How Keystone Herbivores Respond

As discussed above, elevated atmospheric CO_2 consistently causes changes in plant quality that generally reduce the plant's nutritional value for herbivores.

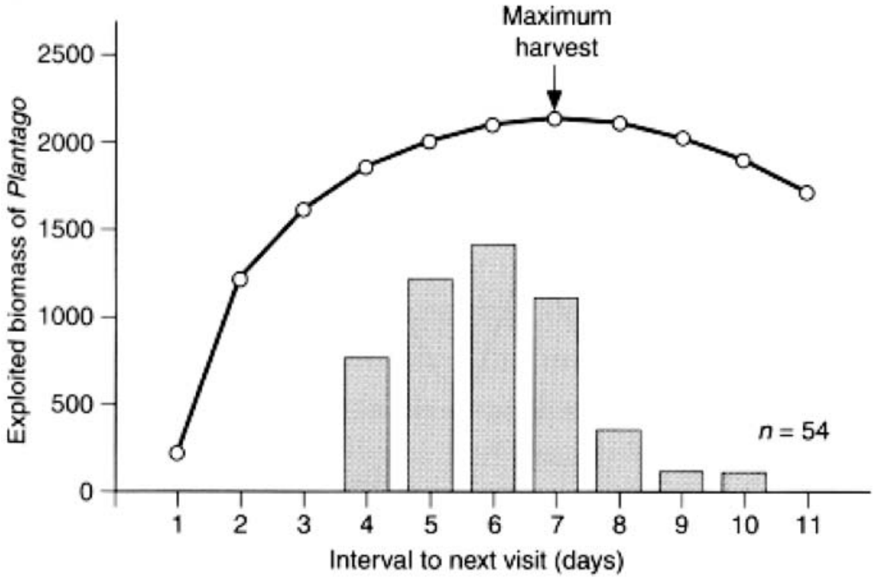


Figure 17.2. Keystone herbivores such as geese sensitively respond to changes in plant quantity. Available biomass of a preferred forage plant (*Plantago maritima*) initially increases with less grazing by brent geese (*Branta bernicla*), as indexed by how often they graze the sward: for example, every day, every other day, and so forth. Maximum harvest by the geese is achieved when they return to a given sward every 7 days, since this allows the plant enough recovery time to allow the geese to maximize their intake rate. Too little grazing of the sward by geese allows the plants to grow beyond the optimal size for maximum harvest, based on a model by Prop (1991). The measured frequency of visits by brent goose flocks to specific swards (shown by the histogram) coincides with maximum harvest but is skewed toward slightly earlier harvest (Prop 1999). From Drent and van der Wal (1999). Reprinted with permission from Blackwell Science.

Since the effects of CO_2 enrichment on the forage quality of plants is predicted to be especially evident in C_3 plants, which predominate in arctic ecosystems, the effect of reduced forage quality on arctic herbivores is particularly pertinent yet poorly understood (Dormann and Woodin 2002). Most research on the response of herbivores to plants treated with CO_2 has focused on insect herbivores inhabiting temperate systems (reviewed by Lincoln, Fajer, and Johnson 1993; Lindroth 1996). We are unaware of any research that focuses on the response of arctic herbivores to changes in plant quality directly caused by elevated atmospheric CO_2. Thus, we will focus here on how arctic herbivores respond to forage with increased plant fiber and decreased protein since these are the expected changes in quality of plants grown under conditions of elevated CO_2.

During the breeding season in the Arctic, adult geese and goslings select plant

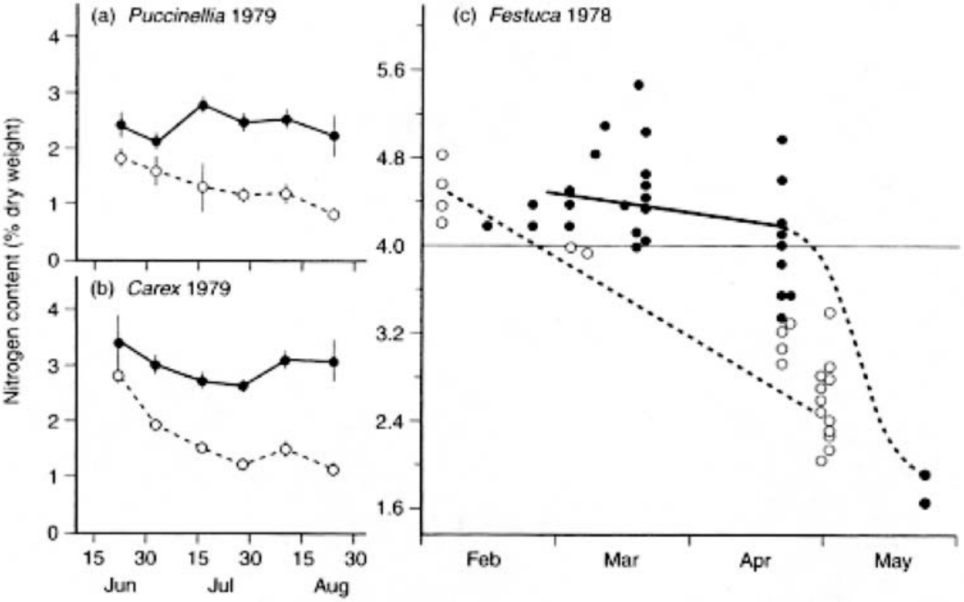


Figure 17.3. Grazing by keystone herbivores such as geese improves plant quality. Nitrogen content of three arctic plant species **(A)** *Puccinellia phryganodes*, **(B)** *Carex subspathacea*, and **(C)** *Festuca rubra* normally decreases during the growing season when plants are ungrazed (*open circles*). Moderate grazing by geese (*solid circles and lines*) delays the decline in nitrogen content of the three plant species and hence extends the period of time with good forage quality. During the summer breeding season, more days with high-protein, low-fiber forage increases growth, survival, and productivity of geese. Data for 1978 are from Cargill and Jefferies (1984), and the data for 1979 are from Ydenberg and Prins (1981). From Drent and van der Wal (1999). Reprinted with permission from Blackwell Science.

species and plant parts that are high in protein and low in fiber (Sedinger and Raveling 1984; Gauthier and Bedard 1990; Krapu and Reinecke 1992; Fox 1993; Laing and Raveling 1993; Manseau and Gauthier 1994). High-quality forage (low fiber, high protein) is needed by geese and goslings during this time to satisfy the high nutrient requirements for breeding and growth, respectively (Sedinger and Raveling 1986; Sedinger 1992). Protein content is an important nutrient because nitrogen is typically a limiting nutrient for herbivores (Mattson 1980), especially during growth and reproduction (Robbins 1993), and geese are relatively inefficient at retaining dietary protein (Sedinger 1997). Fiber content is important because it largely determines digestibility of forage and may limit food intake (Sedinger and Raveling 1988; Sedinger 1997).

The requirement for high-quality forage should make it difficult for avian herbivores such as geese to survive when plant quality and quantity diminishes as predicted with elevated CO_2. Few studies have directly tested how wild herbivores respond to reduced forage quality. Small mammalian herbivores (e.g., voles) increase intake and passage rates and reduce fiber digestibility when eating higher fiber diets (Batzli, Broussard, and Oliver 1994; Cork 1994; Owl and Batzli 1998). This potentially important adjustment in intake and digestibility in response to changes in dietary fiber has rarely been studied in avian herbivores (McWilliams 1999). In one of the few such studies, Japanese quail increased daily food intake with increased dietary fiber, as predicted, although digestibility did not change (Savory and Gentle 1976a,b). More recent studies showed that quail increased their food intake when fed diets with 15% neutral detergent fiber (NDF) compared to diets with less fiber, but they decreased their food intake when fed higher-fiber diets (Starck 1999).

To address how extant avian herbivores respond to reduced-quality forage, we fed Canada goose and lesser Snow goose goslings from hatch until at least 100 days old on one of six diets that were a factorial combination of two levels of fiber and three levels of protein. All birds received the same dietary fiber levels (either 45% or 30% NDF) throughout growth. Levels of dietary protein were high (18%), medium (14%), or low (10%) for goslings after 21 days old. The levels of dietary protein and fiber were chosen based primarily on ecological relevance and nutritional adequacy. In short, the lower level of dietary fiber was representative of selected foods of wild goslings, whereas only a few selected wild foods contained as much fiber as those in our higher level of dietary fiber (Sedinger 1992). We expected this higher level of dietary fiber to increase processing time and thus potentially limit food intake of goslings. The levels of dietary protein were at or below expected protein requirements (ca. 18%) of young growing goslings based on studies of domestic waterfowl (NRC 1984).

All diets were formulated from the same five ingredients: beet sugar (*Beta vulgaris altissima*), soybean (*Glycine max*) meal, orchard grass (*Dactylis glomerata*) hay, oat (*Avena sativa*) hulls, and wheat (*Triticum aestivum*) middlings (a flour byproduct). Use of these ingredients insured that the dietary fiber was primarily from grasses as it is for wild goslings (Sedinger 1992). The following measurements were made on each gosling every 2 to 3 days after hatch until they were at least 100 days old or until growth was complete: body mass, culmen, tarsus, head length, and length of ninth primary (Dzubin and Cooch 1992).

Diet quality affected survival of Snow goslings especially early in growth, whereas diet quality had less effect on survival of Canada goslings (Fig. 17.4). For Snow goslings but not Canada goslings, survival was consistently lower for birds fed the two 10% protein diets and for birds fed the higher fiber diet at each level of dietary protein.

There were also important differences in survival between Snow and Canada goslings fed the same diets. Survival of Snow goslings fed the two 10% protein diets was lower than Canada goslings fed the same diets (LP/HF diet:$\chi 2 = 16.0$, d.f.=1, p=0.0001; LP/LF diet:$\chi 2 = 5.6$, d.f.=1, p=0.02). Similarly, survival

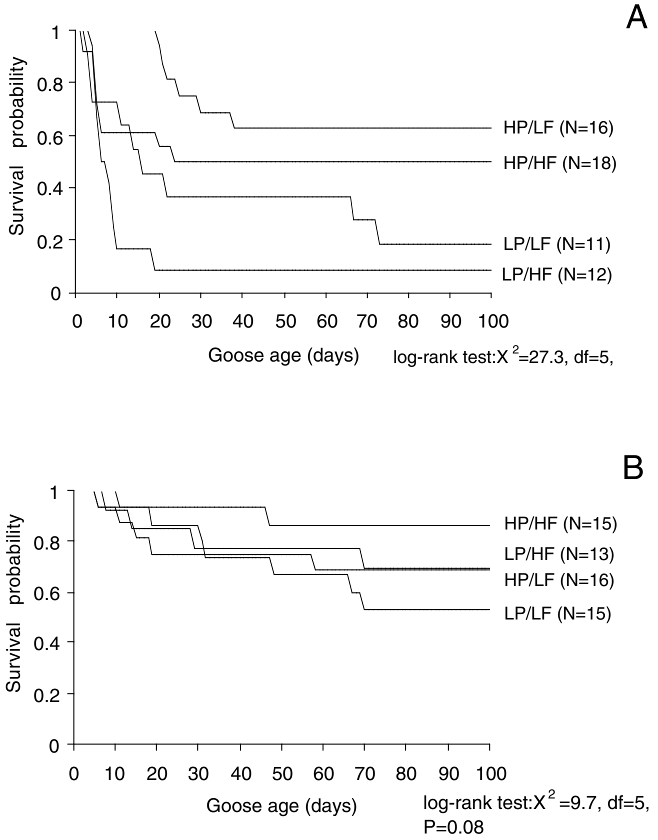
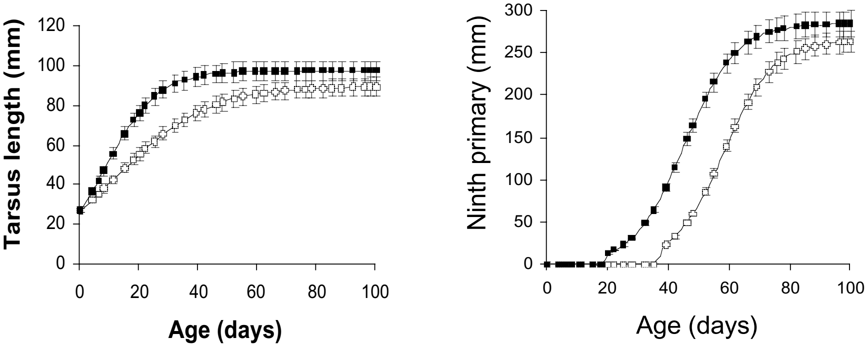


Figure 17.4. Survival probability of Snow geese **(A)** and Canada geese **(B)** fed grass-based diets with either high protein and high fiber (HP,HF), high protein and low fiber (HP,LF), low protein and high fiber (LP,HF), or low protein and low fiber (LP,LF). All geese were fed these diets from hatch until they were at least 100 days old. Survival of Snow goslings was significantly affected by both dietary protein and fiber, whereas survival of Canada goslings was less affected by diet (Kaplan Meir estimates of survival were compared using a log-rank test).

of Snow goslings fed the high-protein, high-fiber diet was lower than Canada goslings fed the same diet ($\chi 2 = 5.3$, d.f.=1, p=0.02). These results suggest that Snow geese have higher protein requirements during growth (>10%) than Canada geese, and that Canada goslings can survive better than Snow goslings when eating diets with more fiber. These results suggest that Snow goslings require a higher quality foraging environment than Canada goslings for normal growth.

Diet quality also affected growth rate and size of Snow and Canada geese (Fig. 17.5). Growth rate and structural size, as indexed by tarsus length, were

A. Canada geese



B. Snow geese

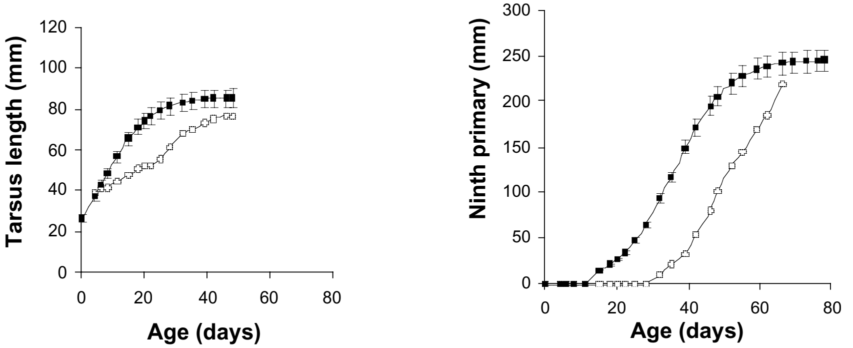


Figure 17.5. Body size (as indexed by tarsus length) and feather growth (as indexed by length of ninth primary feather) of growing Canada geese **(A)** and lesser Snow geese **(B)** fed grass-based diets with either high protein (*solid circles*) or low protein (*open circles*). All geese were fed these diets from hatch until they were at least 100 days old. There was no significant effect of dietary fiber on growth rates (not shown), while geese of both species fed low dietary protein grew slower than geese fed high dietary protein. No standard errors are shown for Snow geese fed low dietary protein because only one Snow gooese survived to at least 60 days when fed that diet.

significantly reduced for both Canada and Snow geese fed the low protein diets. Feather growth, as indexed by length of ninth primary, was also delayed for both goose species fed the low protein diets. We detected no significant effects of dietary fiber on growth of goslings, suggesting geese were able to compensate for this aspect of reduced diet quality.

For arctic-nesting geese, slower growth, smaller body size, and delayed feather growth of goslings is associated with reduced survival and fitness

(Cooke, Rockwell, and Lank 1995; Sedinger, Flint, and Lindberg 1995; Cooch, Rockwell, and Brault 2001) and so these effects of reduced diet quality can have major impacts on goose population dynamics. If elevated CO_2 generally reduces forage quality of arctic plants as expected, then the interspecific differences in nutritional requirements and growth rates of Snow and Canada goslings would suggest that Snow geese would be more affected by reduced forage quality than Canada geese. Thus, the response(s) of such avian herbivores to changes in plant quality and quantity associated with elevated CO_2 is likely to be strongly negative and species-specific.

17.8 Genetic Variation and Phenotypic Plasticity Influence an Organism's Response to Environmental Change

The ability of plant and animal species to respond to environmental change depends on the level of genetic variability within species as well as the ability of specific genotypes to respond flexibly as the environment changes. Arctic plants exhibit substantial ecotypic variation, which increases the chances that some populations will survive when the environment changes (reviewed by McGraw and Fetcher 1992). Arctic herbivores such as Canada geese, *Branta canadensis*, also have substantial ecotypic variation with at least 11 or >100 recognized subspecies depending on the authority (Bellrose 1980; Hanson 1997; Shields and Cotter 1998) and considerable phenotypic variation within subspecies (Leafloor and Rusch 1997).

Phenotypic plasticity (phenotypic variability within single genotypes) may also enable individuals to respond favorably to environmental change (Piersma and Drent 2003). For example, environmental conditions during gosling growth determine adult body size, which, in turn, affects survival and future fecundity (Sedinger, Flint, and Lindberg 1995; Leafloor, Ankney, and Rusch 1998; Cooch, Rockwell, and Brault 2001). In addition, recent work with arctic-nesting geese has demonstrated considerable phenotypic flexibility (reversible phenotypic change within single individuals) in their digestive system that has important ecological implications (McWilliams and Karasov 2001; Piersma and Drent 2003). For example, Snow and especially Canada goslings increase their food intake with increased dietary fiber to compensate for the decrease in digestibility of the higher-fiber diet (Fig. 17.6). A reduction in diet quality is also associated with an increase in digestive capacity (Fig. 17.7), which allows goslings to eat more of the lower quality diet while maintaining digestibility and metabolizability of the diet relatively constant (McWilliams et al. 2000). These same patterns of digestive response in relation to diet quality have been documented for other relatively small herbivores (Cork 1994; Iason and Wieren 1999).

We know little about the extent of phenotypic plasticity and phenotypic flexibility in different species living in arctic ecosystems and its ecological implications. Presumably, species that can flexibly respond are more likely to adapt

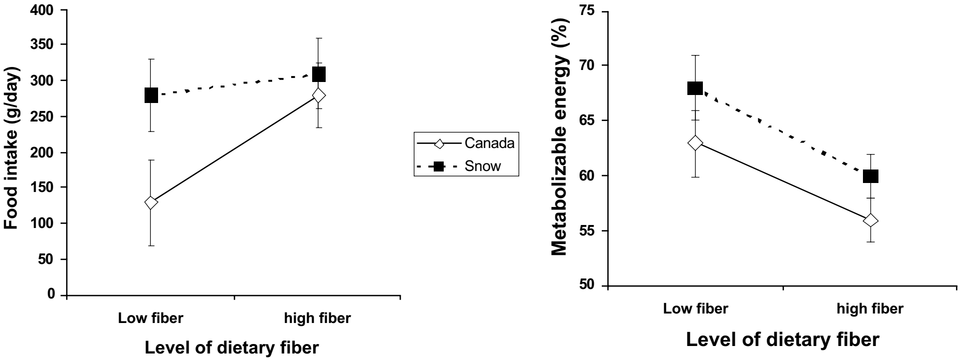


Figure 17.6. Daily food intake (adjusted for goose body mass using ANCOVA) and apparent metabolizable energy of 8-week-old Canada geese and lesser Snow geese fed grass-based diets with either high fiber or low fiber. All geese were fed these diets from hatch until the total collection digestibility trials were conducted when they were 8 weeks old. Canada and Snow geese digested less of the available dietary energy and ate relatively more when fed higher fiber diets. However, the Snow geese with smaller body size increased their food intake only 11% while the larger Canada geese increased their food intake 115% when fed the low-fiber compared to the high-fiber diets. This suggests that food intake of Snow geese may be constrained when they consume high-fiber forage.

successfully to environmental changes compared to other species that are inflexible (Pigliucci 1996; Piersma and Lindstrom 1997). Our results indicate that arctic-nesting geese have significant phenotypic flexibility in their digestive system, yet there is clearly a limit to this flexibility as indicated by their slow growth and reduced survival when fed diets high in fiber and low in dietary protein. For most birds, maximum size of the digestive tract is likely limited by constraints associated with flying (McWilliams and Karasov 2001, 2003). Thus, arctic-nesting geese can flexibly respond to short-term changes in diet quality, but the extent of change in forage quality expected with elevated CO_2 may well exceed their capacity.

17.9 Migration and Mobility Influence an Organism's Response to Environmental Change

Migration of both plants and animals will play a role in the redistribution of arctic biota in response to elevated CO_2 (Davis and Shaw 2001). In general, evidence from past climatic change demonstrates that species migrate individualistically rather than as assemblages, so that autoecological studies should be useful for predicting response(s) of extant biota to future environmental change (Cronin and Schneider 1990; Graham and Grimm 1990; Davis and Shaw 2001).

Arctic herbivores vary tremendously in their mobility with the most sedentary

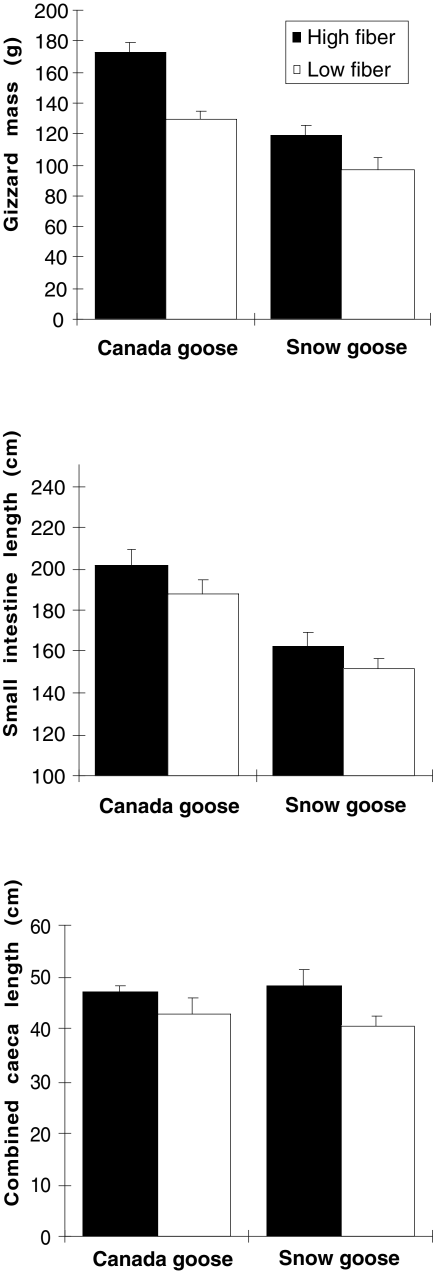


Figure 17.7. Phenotypic flexibility in digestive organs of Canada and lesser Snow geese in response to dietary fiber. Gizzard mass, small intestine length, and the combined length of both caeca increased when geese were fed high-fiber diets compared to low-fiber diets (Factorial ANOVA; Goose species effect: $P<0.0001$ for gizzard and small intestine, $P=0.96$ for caeca; Dietary fiber effect: $P<0.0001$ for gizzard, $P=0.019$ for small intestine, $P=0.004$ for caeca). There was no significant effect of dietary protein on digestive organs (not shown).

(e.g., voles and lemmings) exhibiting dramatic, and often cyclic, population fluctuations, whereas the most mobile (e.g., migratory geese) apparently are able to find preferred habitat when it is available (Boyd and Madsen 1997). If responding to changes in plant quantity and quality simply involves spatially and temporally tracking preferred habitat, then animal species that can outpace the rate of environmental change will survive and those that cannot will perish. Arctic ecosystems are characterized by short growing seasons with high daily rates of plant production (but low annual productivity) even when ambient temperatures are only slightly above freezing (Bliss 1986). In general, birds use their mobility afforded by flight to capitalize on the brief pulse of productivity during the arctic summer—an impressive 15% of the world's bird species breed in the Arctic but then spend the nonbreeding period in more hospitable temperate or tropical climes (Hansell et al. 1998). Thus, arctic-nesting birds provide good examples of highly mobile animals that can effectively track their preferred habitat over relatively large spatial scales (Boyd and Madsen 1997).

However, major changes in plant quantity and quality, and interactions between predators, herbivores, and primary producers are expected with elevated CO_2 that may affect arctic wildlife populations even if they are highly mobile (Root and Schneider 2002). For example, breeding during the short arctic summer requires relatively fast growth rates for especially larger animal species such as geese. Faster growth rates of goslings increase short-term nutritional requirements. Thus, although arctic-nesting geese are quite mobile, their life history is such that large-scale reductions in plant quality and quantity or changes in plant phenology would negatively affect gosling growth and survival unless adaptation occurred. Undoubtedly, the responses of arctic plants and animals to the effects of elevated CO_2 will involve the interplay of both adaptation and migration (Davis and Shaw 2001).

17.10 Summary

Elevated atmospheric CO_2 generally decreases plant quality (i.e., lower protein, increased fiber), especially of C_3 plants such as those that dominate arctic ecosystems. Predicting how changes in the quality and distribution of plants will affect higher trophic levels in arctic ecosystems requires knowledge of the reciprocal interactions between keystone herbivores and their food plants. We review contemporary studies of one group of keystone herbivores in arctic ecosystems, arctic-nesting geese, and their response to changes in plant quality and quantity.

Arctic-nesting geese are good indicators of the health of arctic ecosystems because the ecological limitations associated with being an avian herbivore require them to respond sensitively to changes in plant quality and quantity. Field studies have demonstrated that goslings that grow up in areas with poor habitat quality are smaller as adults and have reduced survival and fitness compared to geese in good quality habitat. Recent captive-rearing experiments with goslings have elucidated some of the important physiological responses of geese to poor quality forage. This recent work emphasizes the importance of phenotypic flexibility in the digestive system of keystone herbivores, and of digestive constraints in determining the lowest quality of food eaten by such herbivores. Thus, predicting the effects of elevated atmospheric CO_2 on arctic ecosystems requires understanding the interplay between phenotypic flexibility, adaptation, and migration of the arctic biota.

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